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A three day meeting, held in Rochester, discussed "Localizing Visual Function in the Brain". The meeting consisted of presentations by 15 prominent scientists of topics including; the anatomy of modular connections in the primate visual system, computational advantages of modular organization, imaging of the function of visual cortex, and physiological and behavioral evidence of modular processing. Each group of presentations was followed by a wide ranging discussion of the theme of the session. An audience of about 200 researchers and students included visual and computational scientists, neurologists and radiologists, as well as a diverse group of investigators (largely physicists and engineers) interested in brain imaging. Many participants felt that it was an unusually productive meeting because of the broad range of related issues covered and the, at times intense, discussions that filled the meeting.

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Final Report

18th CVS SYMPOSIUM
"LOCALIZING VISUAL FUNCTION IN THE BRAIN"
June 18-20, 1992

1. Abstract

A three day meeting, held in Rochester, discussed "Localizing Visual Function in the Brain". The meeting consisted of presentations by 17 prominent scientists of topics including; the anatomy of modular connections in the primate visual system, computational advantages of modular organization, imaging of the function of visual cortex, and physiological and behavioral evidence of modular processing. Each group of presentations was followed by a wide ranging discussion of the theme of the session. An audience of about 200 researchers and students included visual and computational scientists, neurologists and radiologists, as well as a diverse group of investigators (largely physicists and engineers) interested in brain imaging. Many participants felt that it was an unusually productive meeting because of the broad range of related issues covered and the, at times intense, discussions that filled the meeting.

2. Meeting objectives

The meeting was planned to bring together investigators from a wide range of disciplines to explore a common focus of their research, the modular organization of the primate visual system. This is a topic that is studied by neuroanatomists, physiologists, neurologists, computational neuroscientists and physicists, but there is no common venue for communication. Furthermore, many of the participants did not know each other, and often did not know of research approaches that were very relevant to their work. For example, many neuroscientists were not aware of computational work examining the advantages of modular organization of network processing. Likewise, many investigators studying functional imaging were unaware of using radiolabelled agents or optical imaging in macaque monkeys. This meeting introduced many scientists to other researchers and other approaches that complement their work.

3. Content of the meeting

The following is a summary of the addresses given at the meeting. Discussions have not been transcribed, and are therefore not included.

FUNCTIONAL SPECIALIZATION IN THE BRAIN
MITCHELL GLICKSTEIN, University College London

Neuroscience as we know it was formed between 1850 and 1890. Before that time the approaches to understanding the nature of brain function were often vague and confused. By the year 1890 clinicians and neuroscientists thought in an essentially modern way. What theoretical advances and experimental and clinical observations led to our current approach

to the study of structure and function of the brain? There were two fundamental theoretical advances in the second half of the 19th century. One, the neuron doctrine, is the idea that the brain is composed of individual elements which touch but do not fuse. The other was the experimental clarification of the idea of cerebral localization. The brain, especially the cerebral cortex, is made up of different sub-divisions each of which is specialized for a particular function.

I will discuss these developments with particular reference to localization of the visual cortex. The first recognition of anatomical differences between different areas of the cerebral cortex was by Franceso Gennari in 1776, but the function of Gennari's striate cortex was not correctly understood for one hundred years. The first attempt to localize the visual area of the cerebral cortex by David Ferrier was in error. The critical discovery on the role of the occipital lobe in vision was made by Herman Munk in 1881. Munk's discovery was applied to man by Salomon Henschen, Tajsuji Inouye, and Gordon Holmes.

In the past fifty years an ever-increasing number of visual areas outside of the primary visual cortex have been discovered. I believe that current questions about cortical visual organization can be understood more clearly from a historical perspective, and some of the early errors in visual localization can be interpreted on the basis of modern discoveries.

INFORMATION PROCESSING IN THE PRIMATE VISUAL SYSTEM
DAVID C. VAN ESSEN, California Institute of Technology

The visual system of the macaque monkey contains an impressively large number of visual areas that can be identified by anatomical criteria (architectonic and connectional information) and/or physiological criteria (visual topography, receptive field properties, and effects of lesions). Thirty-two distinct visual areas have been identified to date, which together occupy more than half of the cerebral cortex. Several organizational principles guide our understanding of how visual information is represented and processed within the cortex. (1) Distributed hierarchical processing. More than 300 pathways are known to interconnect different visual areas. Based on the laminar patterns of connections, the 32 identified areas can be arranged into an orderly hierarchy containing 10 stages of processing. (2) Concurrent processing streams. Within the cortical hierarchy, several processing streams can be distinguished anatomically, physiologically, and even immunocytochemically. However, there is substantial cross-talk between these streams, and the receptive field properties of neurons in each stream reflect multiplexing of several types of information pertaining to the analysis of form, color, motion, and depth. (3) Form analysis. There is an enormous gulf between the conventional orientation selectivity that is established in V1 and the selectivity for faces, hands, and other complex stimuli that have been reported for some cells in inferotemporal cortex. Indications of an intermediate level of processing in areas V2 and V4 arise from our recent finding of cells selective for concentric, radial, or hyperbolic grating patterns. The use of such nonconventional but precisely defined stimuli may provide a principled way of exploring the neural representation of complex patterns.

VISION, AUDITION, AND SOMESTHESIS: DO THEY ALL SHOW HIERARCHICAL AND PARALLEL ORGANIZATION?
JON H. KAAS, Vanderbilt University

The visual, auditory, and somatosensory systems of higher primates are similar in that they all are characterized by a number of cortical areas. In all three systems, each cortical area is interconnected with several others, and connection patterns can be used to construct hypothetical processing sequences that have hierarchical and parallel components. However, detailed comparisons of the three systems are limited by several factors. First, our present understandings of the organizations of the three systems varies, with visual cortex best understood and auditory cortex least understood. Second, we have only a limited understanding of the extent and nature of species differences in cortical organization. Third, our present understanding of the structural organization of each system is progressing, but there are major uncertainties. For example, current theories of cortical organization of the visual system in monkeys, have basic similarities, reflecting widespread agreement and consensus, and clear differences, which are often ignored or simply considered to be valid differences across species. Another possibility, however, is that the conflicts in theories reflect uncertainties stemming from incomplete and ambiguous data. A related problem is that additional subdivisions of visual cortex are currently being proposed, and these additions need to be evaluated. Another complication is that most of the processing sequences that have been deduced from connection patterns have not yet been evaluated by selectivity deactivating pathways, and results from some of the deactivation experiments to date have been surprising. For example, area MT may not have the expected degree of dependence on inputs relayed from area 17, and the significance of SI inputs to S-II seem to be species variable. Despite these concerns, several important generalizations seem possible. Most notably, all primates appear to have complex processing systems with a number of cortical areas for each modality. While primate taxa may differ in many specific features of these systems, they all have a number of areas and connections in common. Systems for all three modalities have one or more primary or primary-like areas that distribute information directly to several higher level fields, that in turn access additional fields. Deactivation experiments show that primary visual and somatosensory areas are critically important for evoked activity in higher areas. The systems appear to differ in that the visual system has more cortical areas and occupies a larger expanse of cortex than the auditory and somatosensory systems.

IS THERE A COMMON PLAN TO THE VISUAL PATHWAYS OF DIFFERENT SPECIES?
HARVEY J. KARTEN, University of California, San Diego

The central nervous system of most amniotic vertebrates contains multiple telencephalic areas mediating each sensory modality. The multiplicity of visual cortical areas has been most extensively characterized in primates, though they have also been identified in other mammals. Assigning an hierarchical position to each of these cortical regions has provided a useful model, and has prompted a large body of inspired and interesting research on the visual system. However, the current hierarchical model is not easily reconciled with the less extensive, though still growing body of information on the evolution, comparative anatomy, development, and behavioral functions of the different components of the telencephalic visual regions. Thus, in addition to the geniculo-striate pathways, there is also an ancient visual pathway to the temporal lobe independent of inputs from striate cortex. Developmental studies indicate that the temporal pathways develop prior to the geniculo-

striate pathways in rodents and birds. This temporal lobe pathway may be of critical importance in mediating essential and ancient cognitive functions that exist independently of striate cortex. The existence of temporal pathways in parallel with the "newer" striate cortical pathways does not mitigate the significance of hierarchical processing from the striate cortex to the extrastriate cortex. Recognition of areas in receipt of projections from both the striate and temporal "streams" may clarify the "processing functions" of different cortical areas and lead to a more concrete understanding of the role of each of these independent pathways.

HUMAN AND MONKEY VISUAL CORTEX: HOW CLOSE AN ANALOGY?
JONATHAN C. HORTON, University of California, San Francisco

Early in this century, the representation of vision in striate cortex was explored by the clinical examination of soldiers wounded in battle. Inouye and Holmes published maps that assigned 25% of the surface area of striate cortex to the central 15° of vision. We have tested the accuracy of these maps by correlating magnetic resonance images with visual field defects in patients with well-defined lesions in striate cortex. Our findings indicate that central vision is more highly magnified in human striate cortex than reported by Inouye and Holmes, bringing the human map into agreement with data reported from studies in macaque monkey.

We have attempted to use magnetic resonance imaging to elucidate function in extrastriate human visual areas. It is impossible to assign lesions to V2 with surety because of variations among individuals in sulcal and gyral pattern, and in the location and extent of striate cortex. Our efforts to define the V1-V2 border using magnetic resonance to image the myelinated stria of Gennari have been unsuccessful. In some patients, lesions in V2/V3 may be recognized because they produce a characteristic quadrantic visual field defect. It is important to note that small lesions (1-2 cm) outside V1 or V2 do not cause fixed deficits in visual function that are clinically evident.

Cytochrome oxidase histochemistry has proved useful for study of human visual cortex. In specimens from patients with a history of visual loss in one eye, a mosaic of alternating dark and light columns is visible in layer IVC. The layout of the ocular dominance columns resembles the monkey pattern, but the human columns are 2-3 times wider, and consequently human visual cortex contains fewer sets of ocular dominance columns. This difference appears obvious in the cortical representation of the blind spot: in macaques it corresponds to several sets of columns, while in humans it occupies a single megacolumn.

Paradoxically, human striate cortex contains more tissue but fewer hypercolumns than monkey striate cortex. Human occipital lobe measures about 5 times the surface area of monkey occipital lobe, yet human striate cortex is only twice as great in area. Are other human visual cortical areas relatively more magnified than their counterparts in the monkey, or are there more human extrastriate visual areas? Our studies suggest that human visual cortex is not simply a scaled-up version of rhesus visual cortex, but that fundamental differences exist in functional architecture and parcelation.

WHY AND HOW OF MODULARITY: COMPUTATIONAL ADVANTAGES AND A DEVELOPMENTAL PRINCIPLE?
ROBERT JACOBS, Harvard University

As compared to single undifferentiated systems, modular systems frequently show faster learning speeds, better generalization abilities, more interpretable and more adaptable representations, and an economy of hardware usage. One goal of this talk is to specify the computational properties underlying the advantages of modular systems. A second goal is to propose a principle that may underlie the development of modularity in neural systems. Analogous to Darwinian evolutionary processes, it is posited that modules compete for the right to learn to perform a set of tasks. Due to the competition, modules specialize; that is, different modules learn to perform different tasks. The performance and consequences of this competitive principle are studied in amodular connectionist architecture. In particular, we are trying to determine the factors that influence the winner of the competition for each task. Not surprisingly, results suggest that structural correspondences between the modules and the tasks are important.

INTEGRATION OF VISUAL CUES AND LEARNING
TOMASO POGGIO, Massachusetts Institute of Technology

One of the keys to the reliability, flexibility, and robustness of biological vision systems is their ability to integrate several visual cues. During the last several years we have developed Bayesian techniques for integrating different visual cues and implemented them on a parallel supercomputer. The system - the Vision Machine -- achieves model-based recognition on real images through the integration of several early vision modules: edge detection, stereo, motion, texture and color.

In the first part of this talk I will review the Vision Machine project and discuss some physiological experiments (by Nikos Logothetis) motivated by the computational models.

The Vision Machine project suggests the desirability of *learning* vision algorithms and of learning task-dependent integration of learning to classify physical properties of surfaces from the image cues integrated and segmented by the Vision Machine Machine.

More importantly, we have developed a comprehensive approach to learning from examples. We regard learning as a problem of approximating a multivariate function from sparse data -- the examples. We have developed a technique that has its roots in the classical theory of function approximation and has tight and often illuminating relations with other fields such as statistics. Our approach is based on regularization theory, is strictly related to the approximation technique called Radial Basis Functions and is equivalent to a certain class of multilayer networks.

Among the different directions of our work on learning I will describe some speculations on how the visual system may recognize 3D objects, whether simple, high performance visual tasks -- such as hyperacuity tasks -- depend significantly on fast perceptual learning, and I will touch briefly on possible implications for the neurobiology of integration.

OPTICAL IMAGING OF CORTICAL ACTIVITY AND ORGANIZATION
DANIEL Y. TS'O, The Rockefeller University

A particularly promising new development to aid in the study of cortical function is the mapping of cortical activity with optical imaging. Optical imaging offers several advantages over more conventional techniques, such as single-unit recording and 2DG autoradiography. One can map a relatively large cortical region in vivo, obtain successive maps from the same cortex to different stimuli and follow variations in response over time.

To date, most optical recording studies have monitored optical signals provided by extrinsic probes such as voltage-sensitive dyes or other fluorescent indicators. The use of extrinsic probes, while offering important benefits, can lead to major complications, including pharmacological side effects, phototoxicity and uncertainties in staining. We have developed an alternative technique: the optical imaging of the activity-dependent intrinsic (no dye) optical signals. We have applied this technique towards the direct in vivo imaging of the organization of several functional properties of cells in the primate visual areas V1 and V2. This method for localizing features of the functional organization of visual cortex in vivo has proven to be particularly helpful in producing maps to guide the placement of single-unit electrodes and anatomical tracers. We have used this combination of techniques towards the study of color and disparity processing in V1 and V2.

Other variants of optical imaging have been employed in a wide variety of applications, including the imaging of spontaneous and evoked activity at high time resolution and cellular and subcellular recording of cell responses, Modifications of intrinsic signal imaging also hold much promise for chronic behavioral studies in primates, and clinical applications. Thus optical imaging techniques appear to have the potential to span a large range of spatial and temporal resolution requirements.

DOUBLE-LABEL DEOXYGLUCOSE ANALYSIS OF VISUAL CORTICAL COLUMNS
ROGER B. TOOTELL, Harvard University Medical School

We report here on double-label deoxyglucose experiments in anesthetized, paralyzed macaque monkeys. These experiments were designed to clarify the functional organization of cortical visual areas beyond V1 and V2. We were able to label functional columns in eight such areas: VP, V3/V3A, V4, DMT, MT, MST, DP and PIP. Typically two or more types coexist within a given visual area.

Relative to other functional labelling techniques, the double-label deoxyglucose (2ldg) technique has poor time resolution and only two activity labels. On the other hand, it yields excellent contrast (often > 2:1), laminar resolution, good spatial resolution (100 um), and one can see all areas in a given brain, in response to the same visual stimulus. The macaque 2ldg data should be a useful predictor for results expected from functional NMR and PET in man.

Orientation maps were found in V1, V2, VP, and V3/V3A. Extrastriate retinotopic organization was probed by activating vertical vs. horizontal meridia, and upper vs. lower visual fields. Retinotopy was present in V1, V2, V3, V3A, VP, marginally in V4, and there was a patchy representation in MT and MST. Direction columns were found in area MT, but not in V1 (including layer 4B), V2, or other areas, with the possible exception of MST.

We also found many unexpected systems of columns, some functionally related to the V1 blobs or interblobs. In V4, the 2ldg evidence for segregated blob/interblob columns is consistent with intracortical connections (DeYoe and Van Essen, 1990) and unit data (Zeki, 1973; Schein et al, 1982). Another unexpected architecture occurs in MT, where cells with vs. without directional antagonism are organized in columns.

2LDG tests of functional organization in owl monkey found it to be quite similar to that in macaque. Orientation columns are found in V1, V2, MT and perhaps VP. Spatial frequency differences in V1 and V2 are similar to those in macaque. There is a band-interband and a direction architecture in MT. Finally, there is something analogous to the blob/interblob architecture.

Thus, there appear to be a wealth of columns in extrastriate visual cortex. Hopefully, future experiments will characterize the functional nature of the columns better, and reveal the specific connections between the different kinds of columns.

FUNCTIONAL IMAGING WITH POSITRON EMISSION TOMOGRAPHY (PET)
STEPHEN E. PETERSEN, Washington University

Topographic mapping, single-unit recording, and lesion behavior studies have shown that several discrete areas of the brain are devoted to understanding what specializations might exist among the different areas. Functional neuroimaging techniques, such as positron emission tomography (PET), provide an opportunity to address these issues in normal human populations.

The rationale for the use of PET in mapping functional activation is: During the performance of any task, information processing demands are placed on the brain. These demands are met through changes in neural activity in localized regions of the brain. Changes in neuronal activity produce changes in local blood flow. Through the use of PET activation methods, changes in local brain blood flow can be imaged. Given the current resolution of the reconstructed images (~1-2cm) and accuracy of localization (~3-7mm), PET is most effectively used to identify functional areas affected by experimental manipulation, with sub-areal organization (e.g., columnar organization) being currently beyond the scope of the technology.

Most PET studies of the visual system have relied on what might be called "bottom-up" strategies in which the visual input presented to the subject is manipulated to assess how the stimulus attributes are processed by different visual areas. Using this approach, areas have been described in human extrastriate visual cortex that are activated by manipulations of visual motion and color that might be analogous to similar areas described in monkeys (such as MT -MST and V4 respectively).

Another approach that might be taken in assessing specialization of function in visual areas is adopt a "top-down" approach in which visual input is held constant but task demands on the subject are changed. This approach has yielded converging evidence that different areas of human extrastriate cortex are specialized for processing motion, color, and shape information.

FUNCTIONAL IMAGING WITH MAGNETIC RESONANCE IMAGING (MRI)
ROBERT TURNER, National Institute of Health

Magnetic resonance imaging has been used for more than ten years as a means of non-invasively delineating brain anatomy, with excellent spatial resolution. Because time resolution has been poor, and because the primary source of signal is the protons on water molecules, physiological information has not been available from MR images. However, in the last two years an MRI technique under development since 1977, echo-planar imaging (EPI), has opened the door to functional brain mapping.

Three methods of imaging function have been successful. The first uses EPI to observe the passage of a bolus of paramagnetic contrast agent injected into a vein. The relative blood volume in a slice of the brain can thus be deduced, and changes in blood volume related to brain functional activity can be mapped.

The second method, GE-EPI, utilizes contrast inherent in the dependence of the magnetic state of blood on its degree of oxygenation. Deoxygenated blood is significantly more paramagnetic than oxygenated blood. In consequence, a series of echo-planar images spaced at (say) 3-second intervals during performance of a brain task can show the effects of the changes of blood oxygenation caused by changes in blood flow and oxygen utilization. Contrast changes are proportional to the change in total deoxyhemoglobin in the voxel, and the technique is thus sensitive to changes both in blood flow and oxygen extraction.

The third method, IR-EPI, is sensitive mostly to changes in blood flow. It relies on the change of signal caused by variations in the rate at which magnetically-labelled spins in the slice of interest are replenished as perfusion changes.

Successful experiments, mainly using GE-EPI, have been conducted at MGH, NIH, MCW, the University of Minnesota, the Max-Planck-Institut in Gottingen, Germany, and at Siemens Research Labs in Erlangen, Germany. Most of these studies have observed the effects of photic stimulation in human visual cortex, though some have also studied the hand representation in the sensorimotor cortex. The spatial resolution is typically 2 mm x 2mm x 10mm, and the temporal resolution is as low as 0.5 seconds. For repeated stimuli, with gated image acquisition, a time resolution of less than 50 ms may be possible. At the usual static magnetic field of 1.5 T the change of signal is about 2-3% , but increases to 15-25% at a field of 4 T. There is no known biological hazard, and experiments may be repeated as often as desired, since no exogenous contrast agent is used.

Especially at higher magnetic field, these MRI methods appear to offer a very broad scope to novel experiments in human brain function, in particular to understanding the spatio-temporal organization of neural activity in the visual cortex.

ADULT NERVOUS SYSTEM PLASTICITY: CENTRAL VERSUS PERIPHERAL PERTURBATIONS,
TIMOTHY P. PONS, National Institute of Mental Health

Lesion induced cortical plasticity. We previously demonstrated that SII undergoes major functional reorganization 6-8 weeks following total removal of the hand representations in postcentral cortex. But total ablation of a body part representation in postcentral (i.e.

including its maps in 3a, 3b, 1, and 2) results in the absence of somatically driven responses in the representation of the corresponding body part in SII. Interestingly, the SII tissue in question does not remain silent; instead, representations of different body parts in the adjacent portions of SII expand to occupy the partially deafferented cortical zone. For example, following a lesion of the postcentral representation of the hand, there is a greater probability of recording responses in SII to stimulation of the foot. Indeed, the areal extent of the foot representation increases to occupy most of the former hand region (a distance of 5 or more millimeters of cortex).

Cortical plasticity after peripheral deafferentation. As described above, removal of all cortical hand representations in the postcentral strip (areas 3a, 3b, 1, and 2) results initially in the deactivation of the hand map in SII but eventually to the reactivation of the hand map by the foot. To compare the effects of central versus peripheral deafferentation on the pattern of representation in SII, we cut and tied the three nerves normally innervating the hand and, six to eight weeks later, recorded from both SII and the postcentral strip. We found that tissue normally devoted to the postcentral hand representations had become responsive to somatic stimulation of both the arm and face, although stimulation thresholds required to elicit a neuronal response were abnormally high. By contrast, sites in the expected location of the SII hand representation were largely unresponsive to somatic stimulation. The few sites in this region that did respond had receptive field locations and response thresholds that were virtually identical to those in the reorganized portion of the postcentral strip. The results indicate major differences in the way in which body part representations reorganize in SII after peripheral and central nervous system injury.

Plasticity in the postcentral strip following long-standing dorsal rhizotomies. A dorsal rhizotomy is a procedure where sensory nerve roots are severed at the point where they enter the dorsal root ganglion. Such a procedure denervates ascending sensory information to the brain stem, thalamus, and cortex, leaving the motor system completely intact. One might expect the portions of the cortical sensory maps that normally receive inputs from the deafferented region simply to remain deactivated, i.e. unresponsive to somatic stimulation. Until recently, reorganization of cortical maps has been thought to be spatially limited, extending at most across 2.0 millimeters of cortex even several months after deafferentation. We recently had the opportunity to record electrophysiological responses from the cortex of four monkeys that had undergone unilateral or bilateral dorsal rhizotomies 10-12 years earlier. The results from these studies indicate an upper limit of cortical reorganization an order of magnitude greater than previously thought possible, across the entire deafferented cortical region, measuring a centimeter or more in the medio-lateral dimension and at least 6-7 mm in the rostro-caudal plane. This reorganization, unlike that reported previously, greatly exceeds the projection zones of single axons from the thalamus and points to subcortical changes as the likely source underlying the cortical reorganization.

Summary. Preliminary evidence indicates that peripheral nerve manipulations may induce minimal reorganizational changes when compared to central perturbations though further studies need to be conducted to control for the extent of damage, the time course for potential changes after manipulations and possible species differences.

PHYSIOLOGICAL MANIPULATION OF PERCEPTION
WILLIAM T. NEWSOME, Stanford University

Electrical microstimulation techniques can now be used to investigate the influence of physiologically characterized cortical circuits on psychophysical performance. For example, microstimulation of directionally selective neurons in extrastriate area MT can bias a monkey's perceptual judgements of motion direction towards the direction encoded by neurons at the stimulation site. The effects of microstimulation on performance can be substantial, but the direct
activation of neural elements within the cortex appears to be quite local. The latter judgement is supported by three observations: 1) microstimulation effects are topographically restricted to the region of visual space included within the multi-unit receptive field at the stimulation site, 2) the size of a stimulation effect can be altered dramatically by 100-150 micron changes in the position of the stimulating electrode, and 3) increasing the amplitude of the stimulating pulses from 10 to 80 microamps causes a nonspecific deterioration in performance consistent with the simultaneous activation of many cortical columns having different preferred directions. While the neural circuits underlying directional judgements can be accessed locally, the effects of stimulating current must spread through more extensive cortical networks via transsynaptic activation of distant neurons.

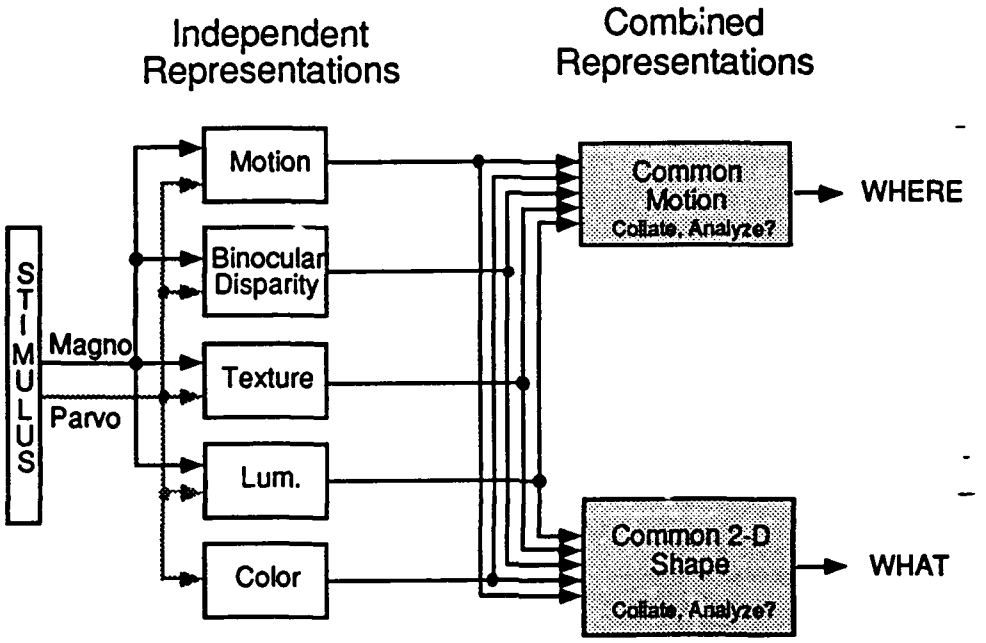
In a recent set of experiments, we applied microstimulation to MT while a monkey performed an eight -alternative, forced-choice direction discrimination task. Motion could appear in any of eight possible directions separated equally by 45 deg. These experiments allowed us to compare the directional tuning of the microstimulation effect with the directional tuning of the visual responses of neurons at the stimulation site. In 25 experiments yielding behavioral effects, the directional choice bias induced by microstimulation was always within the directional tuning curve of the visual responses. Moreover, the bandwidth of the behavioral effect was typically much narrower than that of the visual responses. This narrow bandwidth suggests that the cortex computes a single, most likely direction of motion consistent with the activity in a population of broadly tuned neurons.

DISSECTING VISION WITH PERCEPTUAL STUDIES IN NORMALS
PATRICK CAVANAGH, Harvard University

Many physiological studies suggest that visual information is initially broken into several parallel streams which then recombine to form a common representation. This architecture can be exploited to localize different visual processes. First, we can ask whether a particular task depends on the attribute used to define the stimuli. For example, performance in mental rotation and visual search tasks is basically independent of the attribute used to present the stimuli suggesting that these higher level processes access a common representation. Tests of these processes using composite stimuli (with elements defined by different attributes) support this conclusion.

Another second model for localization experiments comes from studies of interocular transfer: effects that transfer interocularly can be claimed to occur no earlier than area V1 where binocular units first emerge. We can apply this same logic to the independent

processing streams. This simplified figure depicts the convergence of the streams but also suggests the possibility of separate common representations, in this case, one for shape and one for motion.



As shown here, properties such as shape or motion may emerge several times. Interattribute transfer should occur only for properties that emerge at the level of the common representations. Studies of orientation and size show evidence for both independence and transfer, suggesting that these shape properties probably emerge in both the early, independent streams and in the common representation. On the other hand, adaptation and transparency studies of motion do not demonstrate significant independence in our studies suggesting that these aspects of motion processing emerge only at the level of a final common representation.

Finally, contour localization also appears to access information in a common shape representation. When contours defined by different attributes are superimposed, the precision of vernier judgements increases more than would be expected due to probability summation as if the information were being summed before a position decision was made. In addition, when contours defined by different attributes are placed close to each other, they attract each other more or less to the same extent, no matter which attributes are involved. For example, a luminance contour appears shifted toward a color contour to the same extent that a color contour appears shifted toward a luminance contour.

These results suggest that there is only limited independence between the early analyses of stimulus surface attributes such as color, luminance, and texture but that the subsequent final representations for motion and shape integrate the information from earlier analyses in a qualitatively different fashion.

CORTICAL LESIONS IN HUMANS AND MACAQUES· EFFECTS ON VISUAL THRESHOLDS
WILLIAM H. MERIGAN, TATIANA PASTERNAK AND JOHN MAUNSELL, University of Rochester

There is now substantial evidence from both humans and macaques for at least two cortical pathways or processing streams, one of which terminates in parietal and the other in temporal cortex. Details of the anatomy and physiology of cortical areas making up these streams are known for the macaque, and this information and lesion studies suggest a segregation of function. Evidence for separate streams in humans comes from PET functional imaging studies and the difference between the effects of parietal and temporal cortex lesions. This presentation will explore parallels between macaque and human visual cortex by comparing the effects of localized cortical lesions on macaque and human visual thresholds.

There is general agreement that both primate cortical streams originate in area V1, and that they are both damaged by V1 lesions. Lesions of area V1 in macaques resulted in profound visual loss. We were unable to measure any visual detection at the visual field locus corresponding to the lesion, even 10 months after the lesion was placed. Similar loss is found after V1 lesions in humans. Slight residual sensitivity after V1 lesions, termed "blindsight", can often be demonstrated in humans and macaques.

The role of cortical area V2 in the monkey is of great interest because it provides a major output of area V1, and because physiological studies suggest complex neuronal responses. We have studied the effects of V2 lesions in macaques and have found virtually no change in many basic visual capacities, but a severe disruption of complex discriminations. These results suggest a qualitative difference between V1 and V2 in the nature of their visual processing. It is difficult to determine what is a comparable lesion in humans, since the organization and location of cortical areas beyond V1 are not known in humans. Lesions dorsal to V1 cause perceptual problems with the location of objects in space and their movement, while those ventral to V1 disrupt color vision and object and face recognition. Such lesions are unlikely to correspond to V2 lesions in monkeys because they often involve the underlying white matter, and consequently may affect cortical areas far from their location.

We have also studied the effects of lesioning areas MT and MST, two areas which dominate the cortical stream to parietal cortex in monkeys. These lesions produced little or no loss in contrast sensitivity for either detecting, or discriminating the direction of, drifting gratings. However, speed difference thresholds and thresholds for the direction of global motion in noisy displays were elevated. In one monkey, structure from motion discrimination was measured, and was unaffected despite an elevation of speed difference thresholds. Recent studies of humans have found results very similar to these following lesions of lateral parieto-occipital cortex.

In summary, broad parallels in the effects of cortical lesions in humans and macaques suggest that there may be a similar organization of cortical processing in the two. However, much additional evidence will be needed before a compelling case can be made for their similarity or difference.

FUNCTIONAL AND NEURAL DISSOCIATIONS BETWEEN PERCEPTION AND ACTION
MELVYN A. GOODALE, University of Western Ontario

Evidence is reviewed from a number of neuropsychological and electrophysiological studies of the cortical visual pathways to suggest that the neural substrates of what is commonly referred to as visual perception are largely independent of those underlying the visual control of skilled motor output. Thus, patients with optic ataxia following unilateral or bilateral damage to the posterior parietal region are often unable to use information about the size, shape, orientation, and location of an object to control the posture of the hand and fingers and/or the trajectory of their moving limb during a grasping movement even though these same patients can usually identify and describe the very objects they cannot grasp. Conversely, we recently described a patient with visual form agnosia who can direct accurate and well-formed grasping movements towards objects whose qualities she fails to perceive (Goodale et al., Nature 349: 1991). Dissociations of this kind suggest that in normal brains the neural mechanisms mediating visual perception must at some level operate independently from those underlying the visuomotor control of skilled actions of the hand and limb. These neuropsychological data, together with the results of electrophysiological and behavioural studies in the monkey, suggest that the ventral stream of projections from striate cortex to inferotemporal cortex is critical to the visual perception of objects while the dorsal stream projecting from striate cortex to the posterior parietal region mediates the required sensorimotor transformations for visually guided actions directed at those objects. More recent work in our laboratory suggests that perceptual mechanisms participate in motor control when memorial representations are used to drive the required movements or when the controlling stimuli are complex. Thus, perceptual mechanisms are invoked when a delay, even one as brief as 2 s, is introduced between the presentation of the goal object and the initiation of the action. In addition, the more complex the pattern used to control the movements, the more likely it is that perception of those patterns is required before the correct movements can be produced. The action pathway, it appears, uses dedicated modules that work on-line with a limited range of transformational algorithms.

4. Publications

No publication resulted from the meeting for reasons discussed in the application.

5. Participating personnel

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6. Oral presentations

N.A.

7. Registrants

A total of 192 people (including vision researchers, graduate students, and supporting technical staff) attended the symposium. Principal representation was from the disciplines of psychology, neuroscience, cognitive science, computer science, radiology and neurology. Registrants were charged a fee of $90 for admission to the 3-day symposium sessions, except

for students who were charged $50. The whole of the registration fee was applied to reduce the costs borne by the grant.

8. Significance of the meeting

The meeting served several purposes. It introduced investigators, both speakers and non-speaking participants, to work related to theirs that was not widely disseminated across disciplinary lines. In many cases it also introduced them to investigators who were doing that work. The meeting also provided a comprehensive forum for a discussion of issues related to modular neural processing. This was of particular value to students and to investigators considering the relation of their work (e.g. psychophysics) to other neural processing questions. The long-term impact of the meeting will depend in part on the utility of a cross-disciplinary perspective for this field, and on the productivity of personal contacts made by the participants.